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New findings of galeaspids (Agnatha) from the Lower Devonian of Qujing, Yunnan, China

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Abstract New findings of galeaspids (Agnatha) including *Altigibbaspis huiqingae* gen. et sp. nov., an indeterminate polybranchiaspid, *Eugaleaspis changi*, and *Nanpanaspis microculus* are described from the lower part of the Xishancun Formation (early Lochkovian, Early Devonian) near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China. The *Polybranchiaspis*-like new genus is characterized by a blade-like median dorsal ridge on the dorsal side of head-shield. The morphological disparity of the median dorsal ridge and spine in galeaspids suggests that these structures functioned more than providing a hydrodynamic stability. We assume that a high upright and compressed spine may render galeaspid fishes an apparently larger size as seen by a predator, and a blade-like median dorsal ridge may accomplish a defense against the claws of large sea scorpions. *Nanpanaspis* is peculiar in bearing two short laterally projecting processes on each side of the head-shield, and its phylogenetic relationship is discussed based on different interpretations on the homology of these processes. Considering the unique morphology of *Nanpanaspis*, and its early occurrence among the Huananaspiformes, we assign *Nanpanaspis* in the monogeneric family Nanpanaspidae to represent an early branch of the Huananaspiformes.

Key words galeaspids, Lower Devonian, Qujing, Yunnan, China; Xishancun Formation

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1 Introduction

Quijing District of Yunnan Province in South China holds a succession of non-marine Lower Devonian strata (Fig. 1A), which is subdivided into the Xishancun, Xitun, Guijiatun and Xujiachong formations in ascending order (Fig. 1B). The Devonian Xishancun Formation is underlain conformably by the Silurian Yulungssu Formation, and overlain conformably by the

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Xitun Formation (Fig. 1B) (Zheng and Zhang, 1989; Dong, 1992; Zeng et al., 1992; Fan and Liu, 1995; Shan and Wang, 2000). The Xishancun Formation mainly comprises gray-yellow sandstone and siltstone intercalated with silty shale (Fang et al., 1985), yielding a diversified early vertebrate assemblage including galeaspids (Agnatha), placoderms and sarcopterygians (Liu, 1965, 1975; P'an and Wang, 1978; Wang and Dong, 1989; Wang, 1995a, b; Wang, 2000; Zhu, 1992, Zhu and Schultze, 1997; Zhu et al., 1999; Gai and Zhu, 2007; Zhao and Zhu, 2010; Liu et al., 2015; Si et al., 2015). Thus far, 12 genera and 17 species of galeaspids have been known from the Xishancun Formation (Liu et al., 2015; Si et al., 2015). Here, some new findings of galeaspids including *Altigibbaspis huiqingae* gen. et sp. nov., an indeterminate polybranchiaspid, *Eugaleaspis changi,* and *Nanpanaspis microculus* are described from the lower part of the Xishancun Formation near the northeast entrance of Liaokuo Park in Qujing City (Fig. 1C). The new materials were collected by the first author in the 1980s from a siltstone lenticle of less than 1 m^2 large and about 5 cm thickness. The fish-bearing lenticle, which is embedded in a medium-thick layer of yellow sandstone, yielded mainly small galeaspid and placoderm fragments, which indicate a heterochthonous burial. It is noteworthy that the type specimens of *E. changi* and *N. microculus* were erroneously assumed to be from the Xitun Formation in their original description (Liu, 1965, 1975, 1979). Actually, all of them were excavated from the middle part of the Xishancun Formation together with *Szelepis yunnanensis* (Actinolepidae, Arthrodira) at another site of Liaokuoshan (formerly Liaojiaoshan, Liu, 1979).

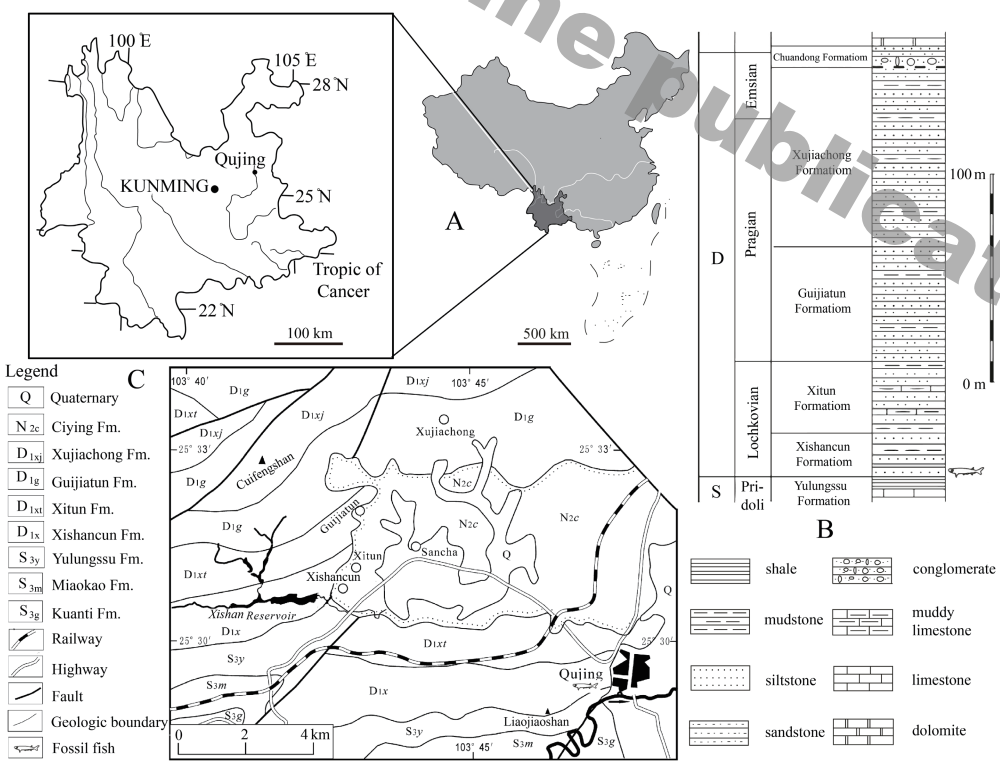

Fig. 1 Locality map and stratigraphic position of the fossil bed yielding *Altigibbaspis huiqingae* gen. et sp. nov. (Modified from Pan et al., 2015; Hao et al., 2007; Si et al., 2015)

2 Systematic paleontology

Subclass Galeaspida Tarlo, 1967

Supraorder Polybranchiaspidida Janvier, 1996

Order Polybranchiaspiformes Liu, 1965

Family Polybranchiaspidae Liu, 1965

Genus *Altigibbaspis* gen. nov.

Etymology The generic name derives from alt (L.), high, gibb (L.), hunchback, and aspis (Gr.), shield, which is often used as suffix of generic name of Agnatha, in reference to the hump profile of the head-shield with the presence of a robust and high median dorsal ridge.

Type species *Altigibbaspis huiqingae* gen. et sp. nov.

Diagnosis As for the type species.

***Altigibbaspis huiqingae* gen. et sp. nov.**

(Figs. 2−3)

Holotype A nearly complete head-shield, IVPP V 20843.1 (Fig. 2A−C).

Paratype An incomplete head-shield, IVPP V 20843.2 (Fig. 2D).

Etymology The specific name honors the late Mrs. Hu Hui-Qing of IVPP, Chinese Academy of Sciences, for her contributions to the exquisite drawings of fossil vertebrates.

Locality and Horizon Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Diagnosis A medium-sized polybranchiaspid with a robust and high median dorsal ridge on the dorsal side of head-shield; the posterior margin of the shield deeply embayed and bearing a dorsal spine in the middle; the inner corners extending backward, well beyond the median dorsal spine; the lateral transverse canals not branching off in their ends; the dorsal commissure anteriorly situated at the first two fifths of the shield.

Remarks The new genus *Altigibbaspis* resembles closely *Polybranchiaspis* in the outline of the head-shield, the relative position of the median dorsal opening and orbital openings, the distribution pattern of sensory canals, and large ornamental tubercles. They differ in the extension of inner corners, the relative position of the dorsal commissure, and the development degree of the median dorsal ridge on the head-shield in particular. The inner corner is moderately developed in *Polybranchiaspis* with its posterior tip level with the end of the median dorsal spine, while the inner corner is greatly developed in *Altigibbaspis*, with its posterior tip well beyond the end of the median dorsal spine. The dorsal commissure is located in the first two-fifths of the head-shield in *Altigibbaspis* and at about midway of the head-shield length in *Polybranchiaspis*. The median dorsal ridge in *Altigibbaspis* is high and robust, keeping the same height almost along its whole trajectory, and sloping down near the posterior margin of the head-shield. By contrast, the median dorsal ridge in *Polybranchiaspis* raises gradually backward along its whole trajectory, and finally projects beyond the posterior margin of the head-shield to form a cone-shaped spine.

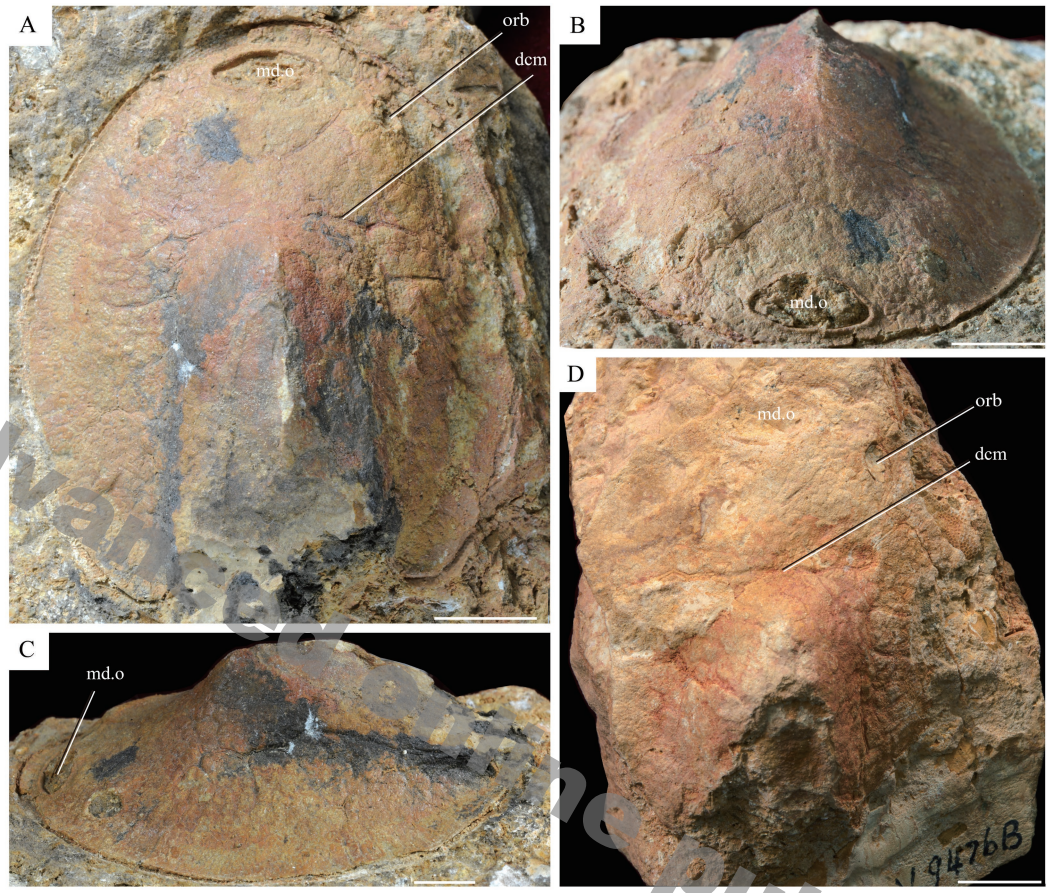

Fig. 2 Photographs of *Altigibbaspis huiqingae* gen. et sp. nov.
A complete head-shield, holotype, IVPP V 20843.1 in dorsal (A), frontal (B) and lateral (C) view;
an incomplete head-shield, paratype, IVPP V 20843.2 in dorsal view (D), Scale bar=1 cm
Abbreviations: dcm. dorsal commissure 背联络管; md.o. median dorsal opening 中背孔; orb. orbital opening 眶孔

Description The new form is a medium-sized polybranchiaspid fish. The head-shield is longitudinal ovoid in shape with a deeply embayed posterior margin. The holotype (V 20843.1) is three-dimensionally preserved with the maximum length of 62.50 mm (from the rostral margin to the tip of the inner corner), the maximum breadth of 52.50 mm, and the maximum height of 17.72 mm (Figs. 2A−C, 3A−C). The paratype (V 20843.2) is an incomplete head-shield, and its preserved portion has the maximum length of 57.50 mm, the maximum breadth of 49.60 mm, and the preserved height of 11.35 mm (Fig. 2D). On the dorsal side of the head-shield, immediately behind the dorsal commissure (dcm, Fig. 3A, B, D), a robust and high median dorsal ridge (md.r, Fig. 3A−D) raises abruptly along the midline. The ridge extends backward horizontally for about 15.90 mm, then slopes down rapidly as it approaches the posterior margin of the head-shield. The ridge looks like a hunchback in lateral view, and becomes blade-like dorsally (Fig. 3B). The posterior margin of head-shield is deeply embayed, and bears a short median dorsal spine (md.s, Fig. 3A, B, D) in the middle. The inner corners (ic,

Fig. 3A, B, D) are broad and lobate, and extend backward well behind the median dorsal spine.

Several sensory organs are visible on the dorsal side of the head-shield. A large median dorsal opening for nostrils (md.o, Figs. 2, 3A, B, D) is set in the anterior part of the head-shield. It is transversal oval in outline with the breadth/length ratio of about 2.0. The long and short axes of the median dorsal opening are 10.97 mm and 5.54 mm respectively in the holotype, and 10.67 mm and 5.75 mm respectively in the paratype. The length ratio between the median dorsal opening and the head-shield is about 0.10, which is evidently smaller than that of most polybranchiaspids. A pair of orbital openings (orb, Figs. 2A, D, 3A, B, D) are anterodorsally placed on the head-shield, but posterior to the median dorsal opening. The distance between orbital openings is 21.00 mm in the holotype. The orbits are round and medium-sized with the diameter range from 4.22 to 5.00 mm in two specimens. There is no pineal opening as in most galeaspids (Liu et al., 2014), and the pineal area shows no difference from the surface around it.

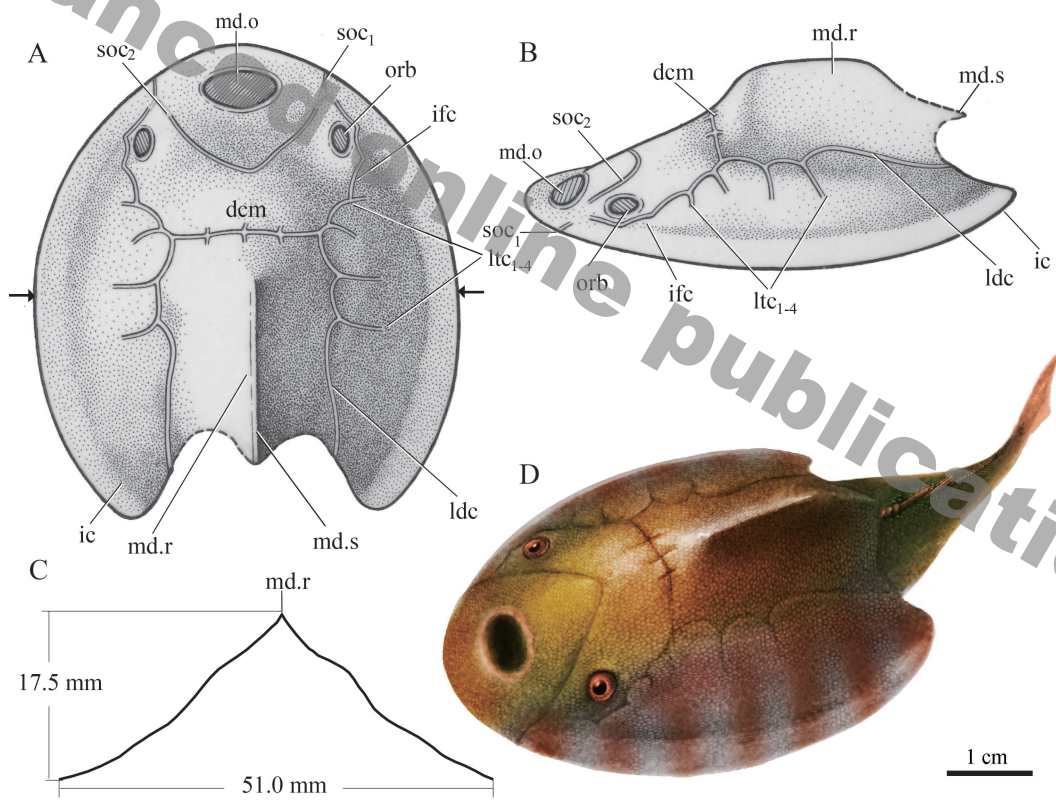

Fig. 3 Restoration of *Altigibbaspis huiqingae* gen. et sp. nov.
A. dorsal view; B. lateral view; C. cross section through the head-shield as arrow indicated in A; D. anterolateral view

Abbreviations: ic, inner corner 内角; ifc, infraorbital canal 眶下管; ldc, lateral dorsal canal 侧背管; ltc_{1-4}. the first to fourth lateral transverse canals issuing from the lateral dorsal canal 从侧背管发出的第一至第四侧横管; md.r, median dorsal ridge 中背脊; md.s, median dorsal spine 中背棘; soc_1, anterior supraorbital canal 前眶上管; soc_2, posterior supraorbital canal 后眶上管; other abbreviations as in Fig. 2

The sensory canals are exposed as grooves. The sensory canal system displays a typical polybranchiaspid pattern in distribution, which includes the supraorbital system (soc_1, soc_2, Fig. 3A, B, D), the infraorbital system (ifc, ldc, ltc, Fig. 3A, B, D) and a dorsal commissure (dcm, Fig. 3A, B, D). The supraorbital system consists of anterior and posterior supraorbital canals. The anterior supraorbital canal (soc_1, Fig. 3A, B, D) reaches the rostral margin anteriorly, and converges posteriorly with the posterior supraorbital canal and the infraorbital canal at a level of the middle of the median dorsal opening. The posterior supraorbital canals (soc_2, Fig. 3A, B, D) of both sides converge posteriorly at a level of the posterior end of the orbital opening, and are V-shaped. The infraorbital system consists of the infraorbital canal (ifc, Fig. 3A, B, D), the lateral dorsal canal (ldc, Fig. 3A, B, D) and four lateral transversal canals (ltc_{1-4}, Fig. 3A, B, D) issuing from the lateral dorsal canal. The dorsal commissure (dcm, Fig. 3A, B, D) is in the first two fifths of the head-shield, and connects the lateral dorsal canals of both sides.

The ornamentation is poorly known from polygonal impressions as the exoskeleton was weathered away. Each polygonal impression is a natural mould of the basal depression of one tubercle (Tong-Dzuy et al., 1995). The polygonal impressions are large and comparable in size with those of *Polybranchiaspis liaojiaoshanensis*, accordingly their ornamental tubercles are probably similar in size.

Polybranchiaspidae gen. et sp. indet.

(Fig. 4)

Referred specimens A fragmentary head-shield, V 20845.1a, and its external mould, V 20845.1b.

Locality and horizon Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Description The referred specimens are a part of head-shield from the posterior margin

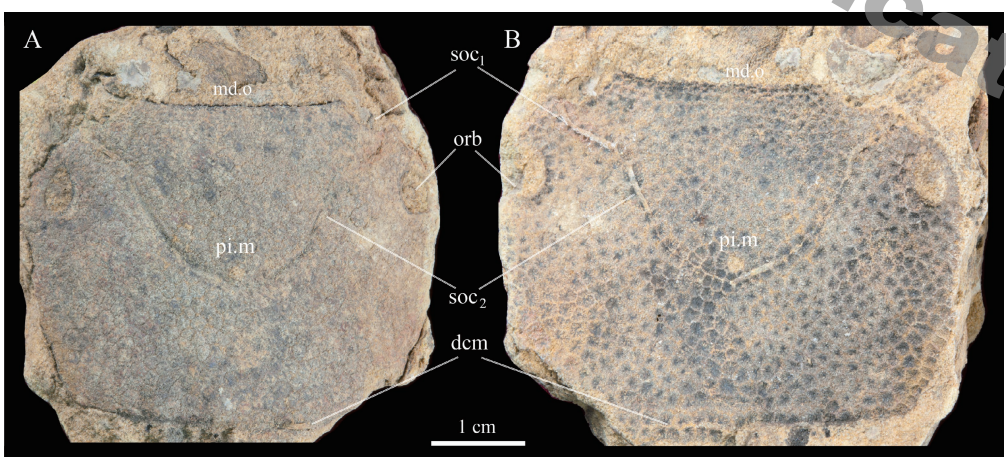

Fig. 4 Photograph of Polybranciaspidae gen. et sp. indet.
A fragmentary head-shield (IVPP V 20845.1a) in dorsal view (A)
and its external mould (IVPP V 20845.1b) in ventral view (B)
Abbreviations: pi.m, pineal macula 松果斑; other abbreviations as in Figs. 2, 3

of the median dorsal opening (md.o, Fig. 4) to the dorsal commissure (dcm, Fig. 4). The long posterior margin of the median dorsal opening suggests that the width of the opening is probably much greater than its length. The orbital openings (orb, Fig. 4) are dorsally placed. The anterior supraorbital canals (soc_1, Fig. 4) join the posterior supraorbital canals (soc_2, Fig. 4), which converge posteriorly at a point just behind the pineal macula (pi.m, Fig. 4) as in most polybranchiaspids. The external mound reveals the ornamental tubercles as large as those in some polybranchiaspids such as *Polybranchiaspis* (Liu, 1965, 1975) and *Laxaspis* (Liu, 1975), but the top of the tubercles is flat rather than pointed as in *Polybranchiaspis* and *Laxaspis*. In the new specimen, the distance from the posterior margin of the median dorsal opening to the dorsal commissure is 33.00 mm. This distance is about the same as that of *L. qujingensis* (32.00 mm) but much smaller than that of *P. liaojiaoshanensis* (21.00 mm).

Order Eugaleaspiformes (Liu, 1965) Liu, 1980

Family Eugaleaspidae (Liu, 1965) Liu, 1980

Genus *Eugaleaspis* (Liu, 1965) Liu, 1980

Species *Eugaleaspis changi* (Liu, 1965) Liu, 1980

(Fig. 5)

Galeaspis changi Liu, 1965; Liu, 1975.

Eugaleaspis changi Liu, 1980.

Holotype A complete head-shield and its natural mould, IVPP V 2981.

Referred specimens An incomplete head-shield IVPP V 20844.1a and its natural mould V 20844.1b; a fragmentary head-shield V 20844.2a and its natural mould V 20844.2b.

Locality and horizon Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Description The specimen V 20844.1a is an incomplete head-shield with the corners missing (Fig. 5A), and its natural mould V 20844.1b (Fig. 5B) preserved the posterior margin of the head-shield. Only a fragment of the left side of the head-shield is preserved in V 20844.2a (Fig. 5C) and its natural mould V 20844.2b (Fig. 5D). Like the holotype of *Eugaleaspis changi*, the new specimens bear a longitudinal slit-like median dorsal opening, of which the length is about 6 times the breadth (md.o, Fig. 5A, E). Other resemblances include the distribution pattern of the sensory canals and the size. The anterior supraorbital canals (soc_1, Fig. 5A, E) are nearly parallel to the median dorsal opening and do not connect with the posterior supraorbital canals (soc_2, Fig. 5A, E). The head-shield length in midline is 36.50 mm in V 20844.1a, approaching that of 37.50 mm in the holotype V 2981 (Liu, 1965). As the head-shield of galeaspids is a sutureless carapace, they probably acquire their bony skeleton only at full growth and therefore each species has a limited size range. The positions of the orbital openings, the median dorsal opening and the pineal macula are also the same as those of the holotype. It is noteworthy that the so-called “pineal opening” in the holotype in the original description (Liu, 1965, 1975) is actually an artificial pore, because a pineal macula does appear in the natural mould of the holotype (Liu et al., 2014).

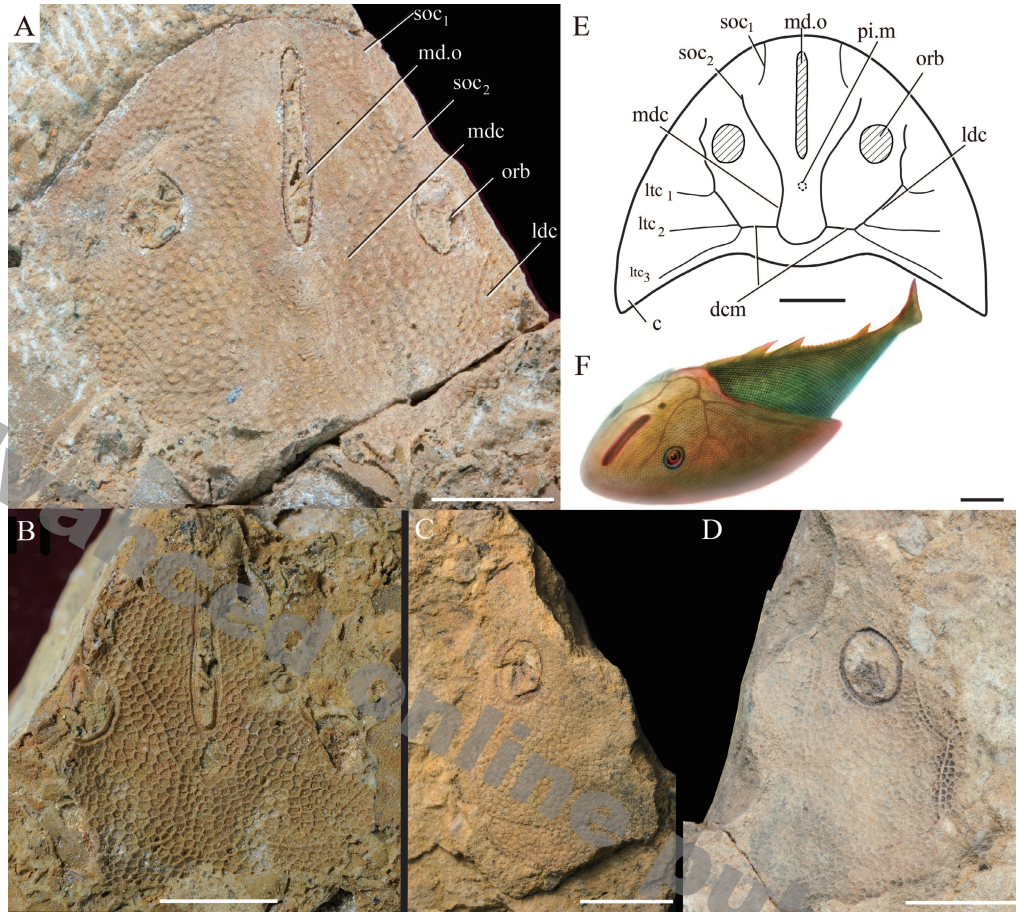

Fig. 5 Photographs (A−D) and restorations (E−F) of *Eugaleaspis changi*
An incomplete head-shield (IVPP V 20844.1a) in dorsal view (A) and its external mould (V 20844.1b) in ventral view (B); A fragmentary head-shield (V 20844.2a) in dorsal view (C) and its external mould (V 20844.2b) inventral view (D); restoration of the head-shield in dorsal view (E) (from Liu et al., 2015); restoration of the whole fish in antero-lateral view (F), Scale bar= 1 cm
Abbreviations: c. corner 角; mdc. median dorsal canal 中背管; other abbreviations as in Figs. 2, 3

Order Huananaspiformes Janvier, 1975

Family Nanpanaspidae Liu, 1975

Diagnosis (emended) Head-shield pentagonal in shape, with a rostral process. Corners small, anteriorly placed (lp.a, Fig. 6A, C); the portion of the head-shield posterior to the corner as long as twice the portion anterior to the corner; the sinus (not, Fig. 6A, C) behind the corner facing laterally and notch-like along the lateral margin of the head-shield; median dorsal opening longitudinal oval; orbits small, dorsally placed, and close to the midline of the head-shield; branchial fossae about ten or more pairs.

Genus *Nanpanaspis* Liu, 1965

Species *Nanpanaspis microculus* Liu, 1965

***Nanpanaspis microculus* Liu 1965**

(Fig. 6)

Holotype A head-shield lacking the posterior margin, and its natural mould, IVPP V 3030.

Referred specimen A natural mould of the fragmentary head-shield, IVPP V 20846.

Locality and horizon Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Description The new specimen is preserved as a natural mould of the visceral side of the anterior part of the head-shield. As in the holotype of *Nanpanaspis microculus* (Fig. 6A), the rostral process (ro, Fig. 6B) of the new material is narrow and short, and the rostral margins of both sides of the head-shield are at an angle of about 100°. The new specimen is also identical with the holotype in the longitudinal oval median dorsal opening (md.o, Fig. 6A, B) and the dorsally placed small orbital openings (orb, Fig. 6A, B).

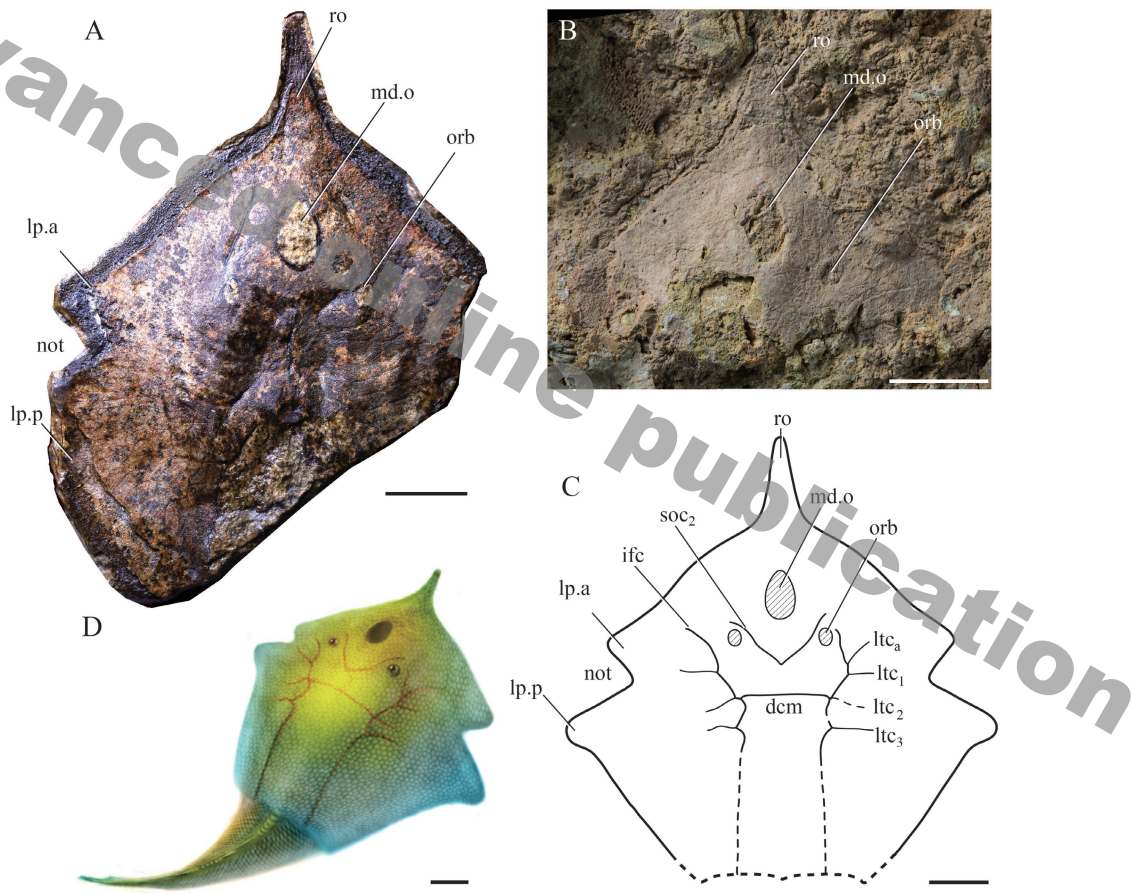

Fig. 6 Photographs (A–B) and restorations (C–D) of *Nanpanaspis microculus*
A. an incomplete head-shield lacking the posterior margin, holotype, IVPP V 3030, dorsal view; B. a fragmentary head-shield, IVPP V 20846, dorsal view; C. restoration of the head-shield (from Liu et al., 2015), dorsal view; D. restoration of the whole fish, antero-lateral view, Scale bar=1 cm
Abbreviations: lp.a. anterior lateral process 前侧突; lp.p. posterior lateral process 后侧突; ltc_a. the first lateral transverse canals issuing from infraorbital canal 由眶下管发出的第一侧横管; not. notch between anterior and posterior lateral processes 前后侧突间的凹槽; ro. rostral process 吻突; other abbreviations as in Figs. 2, 3

3 Discussion

3.1 Morphological disparity of median dorsal ridge and spine in galeaspids

The median dorsal ridge (md.r, Fig. 7A−C) is widely present in galeaspids except eugaleaspidiforms, and can be morphologically classified into three types (Fig. 7). In the first type, the ridge (md.r, Fig. 7A) starts just behind the dorsal commissure, rises gradually, and projects beyond the posterior margin of the head-shield to form a cone-shaped spine (md.s, Fig. 7A). This type is widely seen in *Hanyangaspis* (Pan, 1986, dsp:fig. 3A), many polybranchiaspids such as *Polybranchiaspis* (Liu, 1975, d.sp:fig. 5), *Laxaspis* (Liu, 1975, d.sp:fig. 6), *Damaspis* (Wang and Wang, 1982a, dsp:fig. 1), and most huananaspids such as *Huananaspis* (Liu, 1973:fig. 3), *Sanchaspis* (Pan and Wang, 1981:fig.1), and *Antiquisattiaspis* (Liu, 1985:fig. 1). In the second type, the median dorsal ridge (md.r, Fig. 7B) starts just behind the dorsal commissure as well, but rises steeply to form a high upright and compressed spine (md.s, Fig. 7B). This type is only found in the two forms, *Siyingia altuspinosa* (Fig. 7B) (Wang and Wang, 1982b) and *Hyperaspis acclivis* (Pan, 1992:fig. 35). In the third type exemplified by *Altigibbaspis*, the median dorsal ridge (md.r, Fig. 7C) is blade-like, and keeps the same height almost in its whole trajectory, but slopes down close to the posterior margin of the head-shield. Most galeaspids are bottom-dwellers on sandy or muddy substrates in marginal marine environment (Janvier, 1996, Gai et al., 2015). The median dorsal ridge probably provides hydrodynamic stability in moderate currents with a less energetic cost, which is functionally analogous to the vertical stabilizer of an aircraft. The morphological disparity of median dorsal ridge and spine probably indicates some additional functions developed in galeaspids. Considering the large aquatic, predatory sea scorpions (eurypterids) from the Xishancun Formation (cover image), e.g., a huge claw of Pterygotidae gen. et sp. indet., which was

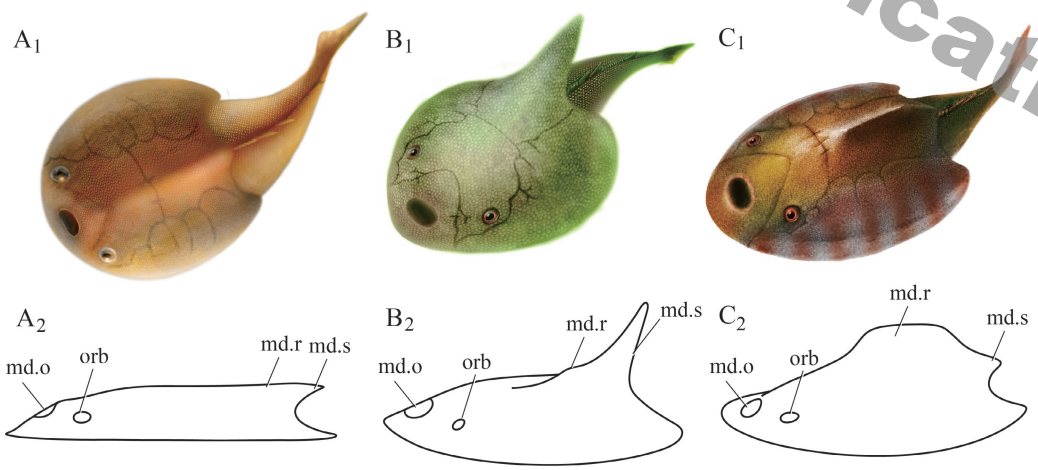

Fig. 7 Morphological disparity of median dorsal ridge and spine in galeaspids
A. *Polybranchiaspis liaojiaoshanensis* in antero-lateral (A_1) and lateral (A_2) view;
B. *Siyingia altuspinosa* in antero-lateral (B_1) and lateral (B_2) view;
C. *Altigibbaspis huiqingae* in antero-lateral (C_1) and lateral (C_2) view
Abbreviations as in Figs. 2, 3. (not scaled)

erroneously assumed to be from the Xitun Formation in its original description (Wang and Gai, 2014), we suggest that a high upright and compressed spine may render galeaspid fishes an apparently larger size as seen by a predator (Janvier, 1996), and a blade-like median dorsal ridge may accomplish a defense against the claws of sea scorpions.

3.2 The phylogenetic position of *Nanpanaspis*

The phylogenetic position of *Nanpanaspis* has been debated all along. When *Nanpanaspis* was erected (Liu, 1965), it was indeterminate in family and order. Liu (1975) proposed a family Nanpanaspidae and an order Nanpanaspiformes for the genus. Janvier (1975) tentatively assigned *Nanpanaspis* to an indeterminate family of the Polybranchiaspiformes, and Zhu and Gai (2006) regarded it as the sister taxon of *Asiaspis* within the Huananaspidae. To a certain extent, the controversy is due to different interpretations of some structures in *Nanpanaspis*. The head-shield of *Nanpanaspis* is roughly pentagonal in shape with a slender and pointed rostral process. Compared with the other galeaspids, *Nanpanaspis* is peculiar in bearing two short laterally projecting processes (lp.a, lp.p, Fig. 6C) and a notch (not, Fig. 6C) between them. Zhu and Gai (2006) suggested that the anterior and posterior lateral processes are homologous with the corner and inner corner of the Huananaspidae respectively (c, ic, Fig. 8A). However, compared with the laterally projecting corner of the Huananaspidae, the anterior process of *Nanpanaspis* is positioned more anteriorly and close to the level of orbital opening (orb, Fig. 8A). Its posterior process is laterally projecting, whereas the inner corner in the Huananaspidae is posteriorly projecting. Therefore, the homology of the two processes of *Nanpanaspis* with the corner and inner corner of the Huananaspidae is not convincing enough.

If the two processes are merely considered as the by-product of the marginal notch without any homology with the corner and inner corner of other galeaspids, *Nanpanaspis* will resemble *Gumuaspis* in the possession of a rostral process and in the absence of the corners (Wang and Wang, 1992). Accordingly, it should be referred to the Polybranchiaspiformes (Fig. 8B).

Another possibility is that the anterior and posterior lateral processes in *Nanpanaspis* are compared to the orbital process and laterally projecting corner in *Lungmenshanaspis* respectively, and the notch is compared to the concave lateral margin of the head-shield in *Lungmenshanaspis* (P'an et al., 1975; Wang et al., 1996). *Lungmenshanaspis*, whose type species is *L. kiangyouensis* (Fig. 8C, middle), was referred to the Huananaspidae (P'an et al., 1975). A prominent process (or.p, Fig. 8C) is set along the lateral margin of the head-shield at the level of the orbital openings (orb, Fig. 8C) in *Lungmenshanaspis*, while the margin from the process to the corner of the head-shield is deeply concave (not, Fig. 8C). Based on this outline, Wang (1991) speculated that there exists a lateral fenestra in each side of the head-shield as in *Qingmenaspis* (Pan and Wang, 1981:fig. 3). He concluded that the orbital process and the concave margin are artificial structures caused by the broken lateral margin of the fenestra. Wang et al. (1996) described another species of *Lungmenshanaspis*, *L. yunnanensis* (Fig. 8C, left) whose prominent orbital process (or.p, Fig. 8C) and concave margin (not, Fig. 8C) are

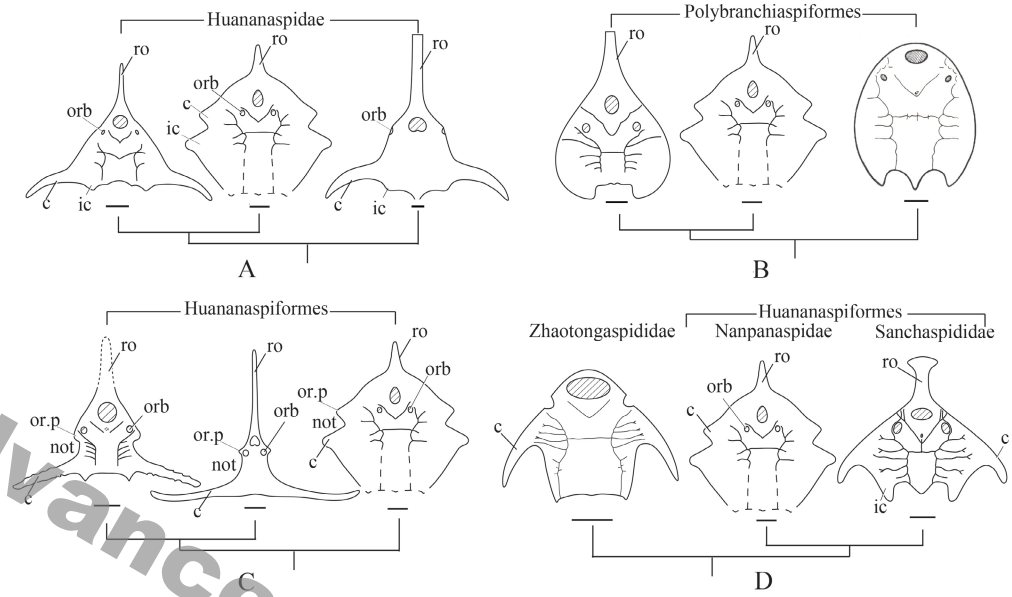

Fig.8 The potential phylogenetic positions of *Nanpanaspis* based on different interpretations of the two laterally projecting processes

A. *Nanpanaspis* sister to *Asiaspis* within Huananaspidae (from Zhu and Gai, 2006);
B. *Nanpanaspis* sister to *Gumuaspis* within Polybranchiaspiformes;
C. *Nanpanaspis* sister to *Lungmenshanaspis* within Huananaspiformes; D. *Nanpanaspis* referred to the monogeneric family Nanpanaspidae provisionally representing an early branch of Huananaspiformes
Abbreviations: or.p. orbital process 眶突; other abbreviations as in Figs. 2−6, scale bar=1 cm

strikingly similar to those of *L. kiangyouensis* (Fig. 8C, middle). The perfect preservation of *L. yunnanensis* indicates that the orbital process and the concave margin are natural structures, particularly considering that the concave margin is equipped with some denticles, which are continually distributed in the corner as well (Wang et al., 1996). Consequently, the so-called "lateral fenestra" does not exist in *Lungmenshanaspis*. The anterior process (or.p, Fig. 8C) of *Nanpanaspis* is strikingly similar to the orbital process of *Lungmenshanaspis*, considering its small size and anterior position leveling with the orbital opening (orb, Fig. 8C). If this homology stands, *Nanpanaspis* could be resolved as a close relative of *Lungmenshanaspis* within the Huananaspiformes (Fig. 8C).

Taking the three possibilities above together, we tend to accept the homologue of the anterior process of *Nanpanaspis* with the corner of the Huananaspidae, but doubt the homologue of the posterior process with the inner corner because the inner corner in the Huananaspidae usually has a position behind the level of the posterior margin of the head-shield, and projects caudally. The notch between the anterior and posterior processes is probably comparable to the armpit-like sinus of other galeaspids such as *Kwangnanaspis subtriangularis* (Cao, 1979:fig. 1; Liu et al., 2015:fig. 99), *Eugaleaspis xujiachongensis* (Liu, 1975:fig.2; Liu et al., 2015:fig. 89). Considering the unique morphology of *Nanpanaspis*, which is hard to be compared to other galeaspids, and its early occurrence among the

Huananaspiformes, we assign *Nanpanaspis* to the mono-generic family Nanpanaspidae, which provisionally represents an early branch of the Huananaspiformes (Fig. 8D).

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云南曲靖下泥盆统盔甲鱼类(无颌类)的新发现

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摘要：本文描述了云南曲靖早泥盆世西山村组盔甲鱼类(无颌类)的新发现，包括一新属、新种——惠清驼背鱼(*Altigibbaspis huiqingae* gen. et sp. nov.), 一件属种未定的多鳃鱼科标本，以及张氏真盔甲鱼(*Eugaleaspis changi*)和小眼南盘鱼(*Nanpanaspis microculus*)的新材料。驼背鱼在很多方面跟多鳃鱼都非常相似，但头甲背面具一特征性的驼背状隆起，其上有一刀刃状的中背脊。中背脊和中背棘在盔甲鱼类里的形态分异度表明：它们除了能够提供游泳方向稳定性外，可能衍生出了一些附加的功能，例如直立高耸的中背棘能使盔甲鱼在捕食者眼里具有了恐吓性，刀刃状的中背脊可能也起到一些防御的作用。南盘鱼头甲侧缘具有两对非常奇特的侧向延伸的突起；通过对这两对侧突同源性的比较，讨论了南盘鱼的潜在系统分类位置。鉴于南盘鱼奇特的形态，以及它在华南鱼目中相对较早的出现时代，建议暂时把南盘鱼放到一个单属科南盘鱼科，代表了华南鱼目早期分出来的一个支系。

关键词：盔甲鱼类，早泥盆世，云南曲靖，西山村组

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